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Research Article

Mapping Risk Zones: niche overlap between *Batrachochytrium dendrobatidis* and endemic amphibians in Mexico's Central-Southern Highlands

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Abstract

Amphibians are amongst the most threatened vertebrate groups worldwide and population declines are driven by climate change, habitat degradation and the spread of emerging infectious diseases. One of the most devastating pathogens is *Batrachochytrium dendrobatidis* (Bd), the causative agent of chytridiomycosis. In Mexico – a global hotspot of amphibian diversity and endemism – Bd has been reported in numerous taxa. However, studies addressing the potential distribution and ecological niche overlap of this species with native amphibians are limited. In this study, we modelled the potential distribution of Bd alongside 13 amphibian species from three families: *Hylidae*, *Ambystomatidae* and *Plethodontidae*. Species were selected, based on their conservation status, endemicity and data availability, particularly for *Pseudoeurycea*, which remains poorly studied beyond presence records. Ecological niche models (ENMs) and niche overlap analyses revealed extensive spatial congruence between Bd and amphibian distributions, especially within the Trans-Mexican Volcanic Belt and Sierra Madre del Sur — regions already recognised as amphibian biodiversity hotspots. Our findings highlight the high environmental suitability of these plants for both Bd and amphibians and reveal critical areas where the risk of disease transmission may increase. These findings emphasise the urgency of implementing targeted conservation actions, including long-term monitoring, early detection of infections, identification of resistant or tolerant populations and regulation of ecotourism in vulnerable regions. Mapping zones of overlap provide valuable guidance for prioritising areas for disease mitigation and habitat protection, particularly for endangered and endemic amphibian species. Our study offers novel insights into the spatial dynamics of Bd in Mexico and contributes to the development of proactive strategies for amphibian conservation.

Key words: *Ambystoma*, amphibian conservation, biodiversity hotspot, endemic species, chytridiomycosis, *Hyla*, *Pseudoeurycea*, niche overlap, Sierra Madre del Sur, Trans-Mexican Volcanic Belt

Introduction

Amphibians are essential components of ecosystems due to their roles in decomposition, primary productivity, nutrient cycling and regulation of insect populations (Hopkins 2007; Hocking and Babbitt 2013). In Mexico, amphibians inhabit a wide variety of ecosystems, including temperate forests (*Pinus* spp.–*Quercus* spp.), cloud forests, tropical forests, grasslands, shrublands and even anthropogenised landscapes (Hernández-Salinas and Ramírez-Bautista 2012; Rosas-Espinoza et al. 2013; Lemos-Espinal and Smith 2020). Anurans represent the most diverse group of amphibians globally, with Mexico hosting approximately 3.69% of the world's anuran species. Caudates (salamanders) form the second-largest amphibian order and are also the second most diverse amphibian group in Mexico (Parra-Olea et al. 2014). Regions with the highest amphibian diversity in the country include the Trans-Mexican Volcanic Belt, Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, the Gulf of Mexico, the Balsas Depression, the Pacific Coast, Soconusco and Oaxaca biogeographic provinces (CONABIO 1997; Arriaga et al. 2000; Parra-Olea 2002; Aguilar-Zúñiga et al. 2008; Pérez-Ramos et al. 2009; Contreras-Calvario et al. 2019; Lemos-Espinal and Smith 2025a; Lemos-Espinal and Smith 2025b). Mexican biogeographic regions, Trans-Mexican Volcanic Belt, Sierra Madre Oriental, Sierra Madre del Sur and Oaxaca harbour the greatest amphibian diversity (Casas-Andreu et al. 1996; Flores-Villela and Goyenechea 2003; Ochoa-Ochoa et al. 2014; García-Padilla 2024).

Three amphibian families stand out due to their diversity in Mexico: *Plethodontidae* is the most diverse, with 140 species (AmphibiaWeb 2025), primarily inhabiting high-elevation forests in the Trans-Mexican Volcanic Belt, Sierra Madre Oriental and the montane regions of Sierra Madre del Sur, Balsas Depression and Oaxaca (Lynch et al. 1983; Parra-Olea 2002). *Hylidae* is the second most diverse family, with approximately 101 *Hylidae* species (Parra-Olea et al. 2014; Canseco-Márquez et al. 2018; AmphibiaWeb 2025). *Ambystomatidae* comprises 12 to 18 species, depending on the taxonomic framework; although it has lower species richness, 16 species are endemic and Mexico represents the centre of diversity for the group (Parra-Olea et al. 2014; Contreras-Calvario et al. 2019; Everson et al. 2021). The nomenclature of species within Hylidae and Plethodontidae in this study follows AmphibiaWeb (2025), whereas species in Ambystomatidae are treated according to Frost (2025), following the species delimitation proposed by Everson et al. (2021).

Amphibians and their habitats are increasingly threatened by deforestation, pollution and urbanisation, which disrupt ecosystem functioning, leading to animal stress and making it easier for more people to enter their habitats and bring in pathogens that are not native and against which amphibians have no natural defences (Frías-Álvarez et al. 2010; Rocha-Santos et al. 2019), such as chytridiomycosis, a serious infectious disease caused by the fungal pathogen *Batrachochytrium dendrobatidis* (Bd) (Ron 2005; Saunders et al. 2012; Becker et al. 2016). *Batrachochytrium dendrobatidis* was first described in 1999 as the causative agent of massive amphibian die-offs. Its presence in Mexico dates back to the 1970s and it is now widespread, particularly in the central and southern regions of the country (Mendoza-Almeralla et al. 2015; Berger et al. 2016).

Like other invasive fungi, Bd requires optimal temperature and humidity conditions to establish and spread (Mendoza-Almeralla et al. 2015, 2016; Sun et al.

2023; Grear et al. 2025). Its broad thermal tolerance enables it to survive, grow and reproduce across various environments, infecting a wide diversity of amphibian hosts (Voyles et al. 2012; Peralta-García et al. 2018). Consequently, Bd has successfully invaded almost all of Mexico and ecological niche modelling has identified the Sierra Madre Oriental, Trans-Mexican Volcanic Belt and Sierra Madre del Sur as biogeographic provinces with high environmental suitability for the pathogen (Ron 2005; Bolom-Huet et al. 2019). *Batrachochytrium dendrobatidis* has been reported to infect at least 50 amphibian species in Mexico, with *Hylidae* and *Plethodontidae* being amongst the most affected families with the largest number of affected species (Mendoza-Almeralla et al. 2015). Within these families, *Hyla*, *Ambystoma* and *Pseudoeurycea* are amongst the most impacted genera, with most of their species distributed across central and southern Mexico (Frías-Álvarez et al. 2008; Mendoza-Almeralla et al. 2015).

Given this context, ecological niche modelling (ENM) and niche overlap analysis have become indispensable tools for conservation planning. These approaches help us to understand species distributions and how they share space and ecological resources — particularly important when native species face threats from invasive pathogens or competitive interactions (Quiroga and Souto 2022; Sunny et al. 2024a, 2024b). Niche overlap analyses are especially valuable for identifying areas of potential ecological conflict, estimating the degree of resource use similarity and predicting local extirpation risks when overlap is high (Letten et al. 2017; van der Veen et al. 2024). In this study, we combined ENM with habitat overlap analysis to examine the spatial distribution and potential resource sharing between *B. dendrobatidis* and 13 amphibian species across central and southern Mexico. We hypothesise that there is a high niche overlap index between the pathogen and the amphibians, suggesting broad potential co-occurrence and highlighting priority areas for surveillance, management and conservation.

Materials and methods

Study area

Amphibian species richness in Mexico exhibits a south-to-north gradient, with the Sierra Madre del Sur recognised as the biogeographic province with the highest overall amphibian richness and endemism (Ramírez-Arce et al. 2022; Flores-Villela and Goyenechea 2003; Lemos-Espinal and Smith 2025a). This is followed by the Trans-Mexican Volcanic Belt (TMVB), which also harbours a high diversity and number of endemic species (Flores-Villela and Goyenechea 2003; Mastretta-Yañes et al. 2015; Lemos-Espinal and Smith 2024). However, the TMVB is also home to the country's most densely populated and urbanised areas (Arriola-Padilla et al. 2015; Heredia-Bobadilla et al. 2017; Sunny et al. 2024a, 2024b; Díaz-García et al. 2025), increasing conservation challenges (Sunny et al. 2018, 2019). This study focused on species distributed across eight biogeographic provinces. We followed the biogeographic regionalisation proposed by INEGI (2013), these units hereafter being referred to as biogeographic provinces due to their correspondence with recognised biogeographic provinces: the Trans-Mexican Volcanic Belt (transition zone which extends across the Mexican states of Colima and central portion of Jalisco, north of

Michoacán, south of Guanajuato, Querétaro and Hidalgo, most of the Estado de México except south, Ciudad de México, north of Morelos, Tlaxcala, most of Puebla except south and the central-western region of Veracruz), Pacific Coast (which extends across the coastal regions of Sinaloa, Nayarit, Jalisco, Colima, Michoacán and Guerrero), Sierra Madre del Sur (transition zone and extends across south Jalisco, southwest Michoacán, most of Guerrero in central and south and south of Oaxaca), Gulf of Mexico (Veracruzan Province, from south of Tamaulipas to coastal Veracruz, Tabasco and Campeche and north or Yucatán), Altiplano Sur (Zacatecana-Potosina Province which extends across north of Guanajuato, Querétaro and Hidalgo, most of Zacatecas and west of San Luis Potosí), Oaxaca (which includes the north of Oaxaca), Sierra Madre Oriental (which includes south-east of Coahuila, south of Nuevo León, south-west of Tamaulipas, north of Puebla and Veracruz) and the Balsas Depression (from centre-south of Michoacán, north of Guerrero, south of Morelos, south-west of Puebla and Estado de México and north-west of Oaxaca) (CONABIO 1997; Aguilar-Zúñiga et al. 2008). These regions were defined as the accessibility area (M area) for ecological niche modelling (Fig. 1).

Species studied

In this study, we included the pathogenic fungus *Batrachochytrium dendrobatidis* (Bd) and 13 amphibian species from three representative genera within the families *Hylidae*, *Ambystomatidae* and *Plethodontidae*. The selected genera and species were *Hyla* (three species: *H. euphorbiacea*, *H. eximia* and *H. plicata*), *Ambystoma* (three species: *A. altamirani*, *A. lermaense* and *A. velasci*) and *Pseudoeurycea* (seven species: *P. altamontana*, *P. gadovii*, *P. juarezi*, *P. lineola*, *P. longicauda*, *P. smithi* and *P. werleri*). Species were selected, based on three main criteria: (1) endemism; (2) conservation status and (3) ecological relevance within the montane regions of central Mexico. All the species are endemic to Mexico and most inhabit high-elevation cloud forests or temperate montane ecosystems – habitats particularly susceptible to climate change, habitat loss and emerging diseases, such as chytridiomycosis (Daszak et al. 1999; Lips et al. 2006; Catenazzi 2015; Sáenz-Romero et al. 2020). From a conservation perspective, the selected species span a broad spectrum of IUCN Red List categories (IUCN 2025): four species are listed as Least Concern (*H. euphorbiacea*, *H. eximia*, *H. plicata* and *A. velasci*); one species is Vulnerable (*P. gadovii*); seven are classified as Endangered (*A. altamirani*, *A. lermaense*, *P. altamontana*, *P. juarezi*, *P. lineola*, *P. longicauda* and *P. werleri*); and one species (*P. smithi*) is listed as Critically Endangered. Notably, most *Pseudoeurycea* species included in this study are extremely data deficient. For several of them, only presence records are available, with almost no information on their population sizes, ecology, reproductive behaviour or physiological tolerances. This data scarcity results in their exclusion from many broad-scale conservation initiatives, despite the likelihood that they are amongst the most vulnerable to environmental disturbance and chronic infections (Cabrera-Guzmán et al. 2021; Sunny et al. 2024a, 2024b; Gómez-Benítez et al. 2025). While salamanders of the genera *Ambystoma* and *Pseudoeurycea* have received some conservation attention, frogs of the genus *Hyla* remain understudied, even though they occupy similar habitats and face comparable threats. Recent vulnerability assessments (Wil-

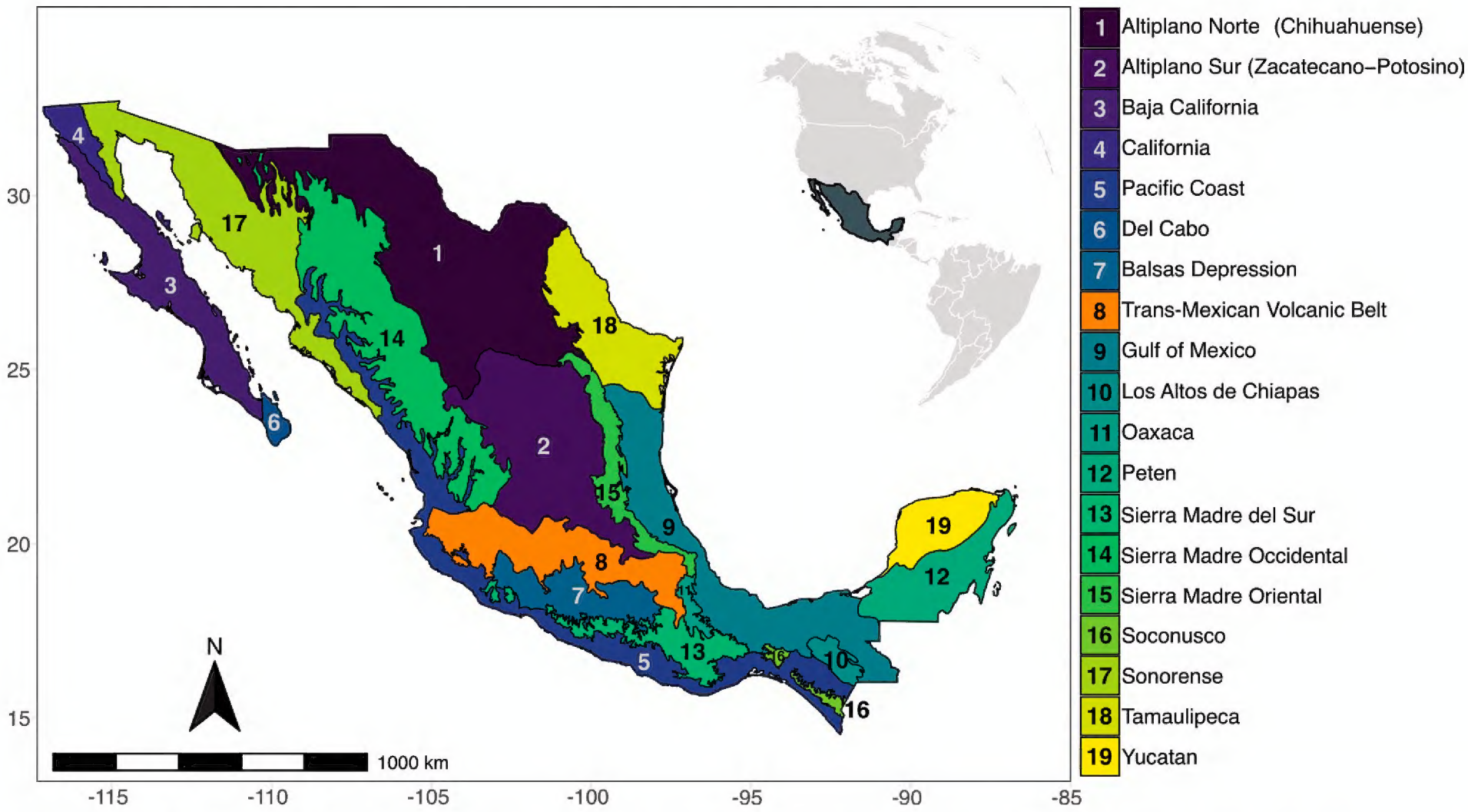

Figure 1. Biogeographic provinces of Mexico, illustrating 19 distinct provinces. The inset map shows the geographic location of Mexico within North America.

son et al. 2013; Sunny et al. 2024a, 2024b) suggest that *Hyla* species may also exhibit moderate to high sensitivity to environmental stressors and should be included in risk assessments and disease distribution models. By including this taxonomically and ecologically diverse group — ranging from broadly distributed species to microendemics with only a handful of records — our study aimed to provide a more integrative and realistic evaluation of the potential impacts of *B. dendrobatidis* across a gradient of conservation statuses and research gaps. This approach highlights not only currently recognised conservation priorities, but also those species that may be highly threatened, yet poorly studied and under-represented in conservation initiatives.

Species occurrence and environmental variables

Occurrence records (geographic coordinates) of all amphibians were obtained from online databases, including the Global Biodiversity Information Facility (GBIF, https://www.gbif.org), iNaturalist (https://www.inaturalist.org) and CONABIO (https://www.gob.mx/conabio).

Occurrence records of *B. dendrobatidis* were obtained from the study by Bolom-Huet et al. (2019), as well as from the associated Dryad data repository (https://datadryad.org/dataset/doi:10.5061/dryad.q50dc8d). Records from 2000 to 2022 were compiled and filtered using the EcoNicheS package for R (Sunny et al. 2025). Initially, records with coordinate errors, those falling outside the known geographic range of the species and duplicates were removed. To minimise spatial autocorrelation and avoid pseudoreplication, the data were spatially rarefied, retaining only one occurrence per 1 km^2 grid cell. This approach has been shown to substantially reduce model overfitting (Sunny 2024). Nineteen bioclimatic variables at a 30 arc-second resolution (~ 1 km)

were obtained from WorldClim version 2.1 (Fick and Hijmans 2017), as was a topographic variable (elevation). In addition, land-cover variables were included, based on their ecological relevance to salamander distributions. A Pearson correlation analysis was conducted using the ENMTools (Warren et al. 2010) and usdm (Naimi 2017) R packages to eliminate highly correlated variables ($r^2 > 0.7$; Dormann et al. (2013)). The following seven final variables were retained: percentage cover of agriculture, arid vegetation, grassland, fir forest, pine forest, oak forest and cloud forest. These land cover layers were derived from the Land Use and Vegetation Series VI (1:250,000 scale), developed by the National Institute of Statistics and Geography (INEGI 2017), based on satellite imagery from 2014 as described in Vargas et al. (2021). An urban settlement layer was also included to define areas of zero habitat suitability, following González-Fernández et al. (2018).

Environmental niche modelling

Two distinct methodologies were employed for distribution modelling to facilitate comparative analysis:

ENMeval: Maximum Entropy Algorithm

We performed ecological niche modelling using the ENMeval package in R, implementing the maximum entropy algorithm in Maxent version 3.3.3 (Phillips et al. 2006). Species-specific settings were used to test regularisation multiplier values of 1 and 2, along with the following feature classes: linear (L), quadratic (Q), product (P), threshold (T) and hinge (H). The tested feature class combinations included L, H, LQ, LQP, LQH, LQHP and LQHPT. A total of 100,000 background points were randomly generated to characterise the environmental background. To reduce spatial autocorrelation and ensure independence between training and testing data, we applied the “block” method from ENMeval, which partitions occurrence data geographically, based on latitude and longitude (Radosavljevic and Anderson 2014). This spatial partitioning ensures that training and evaluation datasets are separated across space (Fig. 1). Model performance was assessed using the corrected Akaike Information Criterion (AIC) for small sample sizes (AICc) and the area under the curve (AUC) of the receiver operating characteristic (ROC) plots. To refine the model evaluation, we implemented partial ROC analyses (Peterson et al. 2008) using the R package ntbox (Osorio-Olvera et al. 2020). Area Under the Curve values were interpreted according to the categories proposed by Hosmer et al. (2013) and response curves for each environmental variable were generated directly from Maxent (Phillips 2021). To generate binary suitability maps and estimate potential species distributions, we applied the 10^{th} percentile training presence threshold for each species.

biomod2

An ensemble model was also constructed with the biomod2 package (Thuiller et al. 2023) implemented in the shinydashboard package EcoNicheS for R. Ten algorithms available in the package were selected. These models included the

generalised linear model (GLM), generalised boosting model (GBM), generalised additive model (CTA), artificial neural network (ANN), surface range envelope or BIOCLIM (SRE), flexible discriminant analysis (FDA), random forest (RF), Maxent, Maxnet and XGBOOST. As presence data were available, a set of 10,000 pseudo-absence data points was randomly generated in EcoNicheS for R. The prevalence was set to 0.5 to ensure the presence or absence of the same importance in the calibration process (Linero et al. 2020). The models were calculated ten times, each run with a different selection of training and testing datasets. The proportion of data for calibration was set to 70% (Linero et al. 2020).

To evaluate the overall model accuracy of both the Maxent and ensemble models, the area under the curve (AUC) from the receiver operating characteristic (ROC) plot was used first (Metz 1978; Phillips et al. 2006), followed by the transformation of the area under the curve (AUC) into a partial receiver operating characteristic (PROC) curve (partial ROC; Peterson et al. (2008)). For this purpose, the package EcoNicheS (Sunny et al. 2025) in R was used. For the ensemble model, the true skill statistic (TSS) was calculated with the package biomod2 (Allouche et al. 2006), based on the sum of sensitivity and specificity minus one (the sensitivity is the proportion of correctly predicted presences and the specificity is the proportion of correctly predicted absences). In the biomod2 approach, the models were assembled by a total consensus rule and algorithms were assembled by the weighted sum of evaluations greater than TSS > 0.8 (Linero et al. 2020; Vargas-Jaimes et al. 2021). The ensemble model (seven algorithms × 10 repetitions) was subsequently used to project the potential distributions of the four species. To evaluate the potential distribution areas of Spiny Lizards, we applied two threshold criteria: the presence of training in the 10^{th} percentile and the presence of training in the 80^{th} percentile. The 10^{th} percentile represents a more permissive threshold, often used to capture the full potential range of a species, including marginal habitats. In contrast, the 80^{th} percentile is a more conservative and ecologically realistic threshold and is especially suitable for assessing vulnerability in the species studied. These analyses were performed using the EcoNicheS package in R.

Niche overlap and linear, blob and ribbon range break tests

Niche overlap between *Batrachochytrium dendrobatidis* and amphibian species from the genera *Hyla*, *Ambystoma* and *Pseudoeurycea* was assessed using multiple metrics, including Schoener's D, Hellinger's I and the Spearman rank correlation coefficient. Additionally, we incorporated newer metrics — env. D, env. I and env.cor — proposed by Warren et al. (2021). These environmental similarity metrics operate in the full n-dimensional environmental space defined by all possible combinations of predictor variables rather than being limited to the realised environmental conditions found in the training region. This approach provides more precise estimates of niche similarity, particularly when lower tolerance values are applied. To test for niche identity, we used a null hypothesis framework in which the environmental occurrences of both species were considered random draws from the same underlying distribution. Since D and I can overestimate similarity when suitability values are uniformly high across the landscape, metrics based on environmental space (env.D, env.I, and env.cor) provide more robust evaluations by accounting for the full

environmental conditions. As highlighted by Sunny et al. (2023), this method reduces biases associated with overlapping high-suitability regions that may not reflect true ecological equivalence. We also applied linear and blob tests to evaluate whether the environmental spaces occupied by two species were more different than expected by chance. Furthermore, ribbon tests were used to assess whether species distributions are separated by unsuitable habitats that may act as dispersal barriers for one or both taxa. All these analyses were conducted using the EcoNicheS platform (Glor and Warren 2011; Sunny et al. 2025), which integrates spatial, statistical and environmental tools for ecological niche modelling and comparison.

To assess the spatial overlap between amphibian species and the chytrid fungus *Batrachochytrium dendrobatidis* (Bd), we used the terra package in R to process and analyse the raster data. First, we imported the predicted habitat suitability map for Bd and binarised it using a fixed threshold of 0.16, chosen for its ecological relevance. This yielded a binary raster indicating the presence (1) or absence (0) of Bd. Subsequently, we loaded the binarised distribution maps for 13 amphibian species, each of which was subjected to a threshold using the 10^{th} percentile training presence rule obtained from the ENMeval model outputs. All the rasters were standardised and managed as multilayer SpatRaster objects.

For each species, we conducted cell-wise multiplication between its binary distribution map and the Bd binary layer. This operation allowed us to delineate and quantify areas of predicted co-occurrence where both the species and Bd were simultaneously present. The resulting overlap maps were visualised using red colour gradients, with darker shades denoting stronger overlap. All raster visualisations were generated using terra and arranged in multi-panel layouts to enable interspecies comparisons. These analyses revealed regions across the Trans-Mexican Volcanic Belt where amphibians are likely at elevated risk of Bd exposure. To quantify exposure, we calculated the proportion of suitable habitat for each species that overlapped with the binarised Bd raster. This overlap metric, expressed as a percentage, was computed from the total number of overlapping cells relative to the total number of suitable cells for each species. The results were visualised using horizontal bar plots generated with ggplot2, facilitating comparisons across species.

We also developed a composite vulnerability index by integrating spatial exposure information with information from The International Union for Conservation of Nature (IUCN) Red List categories. Each threat category was assigned a numeric score (least concern = -2, vulnerability = -1, endangered = +1 and critically endorsed = +2) and this score was combined with the standardised overlap percentage to yield a single vulnerability index per species. These indices are visualised as colour-coded bars representing IUCN status (green = least concern, orange = endangered, red = critically endangered). To explore multivariate patterns of vulnerability, we performed a principal component analysis (PCA) using two standardised variables: (1) the percentage of spatial overlap with Bd and (2) the numeric IUCN threat category. Principal Component Analysis, conducted using the prcomp function in R, revealed that the first two components accounted for 92.3% and 7.7% of the variance, respectively. Species positions in the biplot were coloured, based on their composite vulnerability index, using a gradient from black (least vulnerable) to yellow (most vulnerable), with visualisation handled via ggplot2 and the viridis palette.

Finally, to identify areas where Bd suitability coincided with amphibian richness, we created a species richness raster by summing the 13 binarised species maps. These rasters were aligned to a common grid using the terra package. We overlaid the continuous Bd suitability raster (0–1 range) on the richness map using terra::mask and terra::crop, isolating values only in areas where at least one amphibian species was predicted to occur. The resulting map highlights biodiversity hotspots that are simultaneously suitable for Bd, representing areas of heightened conservation concern. The colour gradients indicate amphibian richness and Bd overlap intensity, respectively, produced using ggplot2 and rasterVis.

Results

Ecological niche modelling

After filtering the data, 14 records were obtained for *P. altamontana*, 34 for *P. gadovii*, 55 for *P. juarezi*, 55 for *P. lineola*, 15 for *P. longicauda*, 45 for *P. smithi* and 20 for *P. werleri*; 89 for *A. altamirani*, 48 for *A. lermaense*, 135 for *A. velasci*, 58 for *H. euphorbiacea*, 53 for *H. eximia*, 76 for *H. plicata* and 50 for *B. dendrobatidis* (Fig. 2).

According to the ENMeval, the models were the combinations L, LQ and LQH with regularisation multipliers of 1–2 (Table 1). The Maxent models performed better than expected according to random AUC (0.9135–0.9969; p values ≤ 0.0001); partial ROC bootstrap tests generated significant ratios of the empirical AUC to the null values (AUC ratios ≥ 1.567745; p values ≤ 0.0001) (Table 1). The most important environmental variables related to the 13 amphibian species were the maximum temperature in the warmest month (Bio5), the minimum temperature in the coldest month (Bio6), the precipitation in the wettest month (Bio13), the precipitation in the driest month (Bio14), elevation, *Pinus* forest percentage, *Quercus* forest percentage, agricultural percentage, forest

Table 1. Predictive performance of the 17 ENMeval models of potential distributions for 14 amphibian species.

	ROC	rm	fc	AUC train	Or.10.avg	AICc
A. altamirani	1.861274	2	LQH	0.9866	0.1136	1863.91
A. lermaense	1.849378	2	LQH	0.9951	0.1277	959.05
A. velasci	1.433084	2	LQH	0.9307	0.1642	3344.47
H. euphorbiaceae	1.679124	2	LQ	0.9392	0.1607	1402.63
H. eximia	1.654106	1	LQ	0.9320	0.1293	1296.86
H. plicata	1.822052	1	LQ	0.9790	0.1600	1682.89
P. altamontana	1.964409	2	LQ	0.9827	0.1180	315.78
P. gadovii	1.734296	2	L	0.9698	0.1493	754.83
P. juarezi	1.689695	1	LQ	0.9675	0.2225	1222.53
P. lineola	1.818388	1	LQ	0.9800	0.1538	1136.47
P. longicauda	1.95531	2	L	0.9795	0.1250	370.11
P. smithi	1.729906	1	LQ	0.9664	0.0909	996.85
P. werleri	1.981272	1	L	0.9969	0.2083	277.60
B. dendrobatidis	1.567745	2	LQ	0.9135	0.16	1272.85

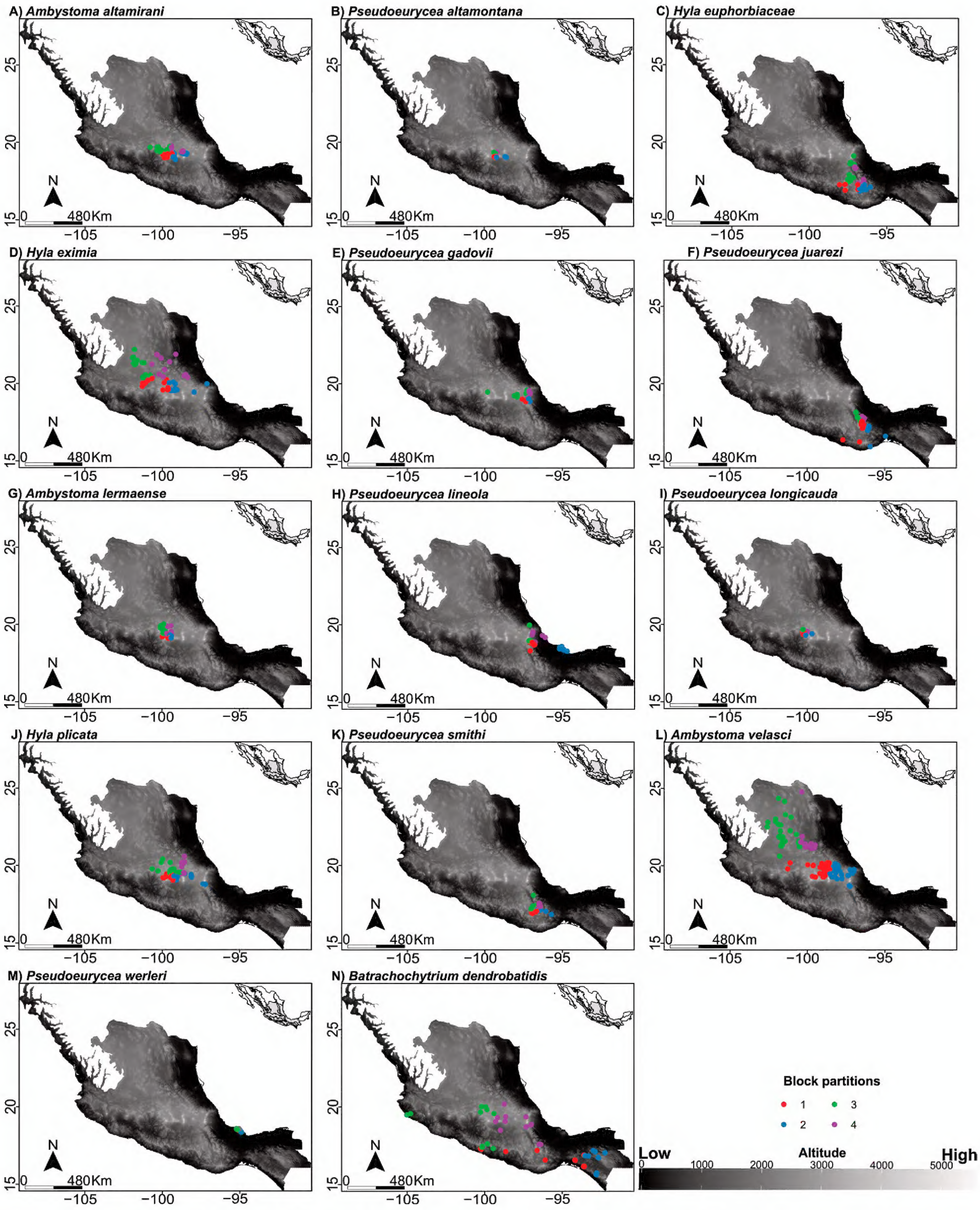

Figure 2. Occurrence records of 14 amphibian species and *Batrachochytrium dendrobatidis* partitioned by the block method, with the accessible area (M) presented in grey.

percentage, grassland percentage and arid vegetation percentage (Fig. 2). For most species, the maximum temperature in the warmest month was a positive variable in the determinate range; for example, *A. lermaense* presented an optimum temperature range of 15–25 °C. The minimum temperature of the cold-

est month was also positive within certain ranges for almost all *Ambystoma* species, except *A. velasci* and the remaining species had an optimal habitat suitability between ≈ -2 °C and 10 °C. Precipitation in the wettest month was positive for most *Ambystoma* species in a given range; precipitation in the driest month was important only for three *Ambystoma* species in given ranges: *A. altamirani* ≈ 10–25 mm and *A. velasci* ≈ 10–20 mm. For *Hyla* species, only the minimum temperature of the coldest month was positive in a given range for *H. euphorbiacea* ≈ 5–8 °C and, for the other two species, was negative; precipitation in the wettest month was also positive in a given range only for *H. euphorbiacea* ≈ 110–210 mm and precipitation in the driest month was important only for *H. eximia* ≈ 5–15 mm. The maximum temperature in the warmest month was positive within a certain range for five *Pseudoeurycea* species: *P. gadovii*, *P. juarezi*, *P. lineola*, *P. longicauda* and *P. werleri*. This species has an optimal habitat range of ≈ 10–30 °C; the minimum temperature in the coldest month was positive within a given range for *P. altamontana*, *P. gadovii*, *P. lineola*, *P. longicauda*, *P. smithi* and *P. werleri* ≈ 3–15 °C; and the precipitation in the wettest and driest months was positive for almost all *Pseudoeurycea* species. For *B. dendrobatidis*, the maximum temperature in the warmest month was positive within a given range of ≈ 15–35 °C and the minimum temperature in the coldest month was a negative variable. Altitude was a positive variable for all species. *Pinus* forest percentage, *Quercus* forest percentage and cloud forest percentage were positive variables for nearly all species; only *H. plicata* (*Pinus* percentage ≈ 10–80%; *Quercus* percentage ≈ 10–70%), *P. lineola* (cloud forest percentage ≈ 10–100%) and *P. gadovii* (*Pinus* percentage ≈ 10–90%) were positive only within a given range. For *B. dendrobatidis*, the *Quercus* forest percentage was positive in a given range of ≈ 10–50%.

The *Ambystoma* species had the highest probability of being present in the TMVB and Altiplano Sur (AS) (Figs 3A, G, L, 4A, G, L); *Hyla* species, in the TMVB; Sierra Madre del Sur and AS (Figs 3C, D, J, 4C, D, J); and *Pseudoeurycea* species, in the TMVB and Sierra Madre del Sur (Figs 3B, E, F, H, I, K, 4M, B, E, F, H, I, K, M). The *B. dendrobatidis* population is likely to be distributed in the TMVB, Sierra Madre del Sur and Sierra Madre de Chiapas (Figs 3N, 4N). According to the 10th percentile training presence threshold, *B. dendrobatidis* had the greatest distribution amongst all the amphibians studied: 267, 557.2 km^{2,} and the most restricted *P. altamontana*, with 9,982.09 km^2 (Table 2).

Niche overlap, linear, blob and ribbon range break tests

According to the environmental niche overlap analysis, most species pairs exhibited non-significant niche similarity test results ($p > 0.05$), indicating that observed niche overlap values did not differ statistically from random expectations (Table 3). Therefore, niche relationships are described here in comparative and qualitative terms, based on the magnitude of overlap indices (Schoener's D and Hellinger's I), rather than on statistical significance. Amongst the analysed species, *Batrachochytrium dendrobatidis* (Bd) and *Ambystoma altamirani* showed relatively higher overlap values (D = 0.423; I = 0.572), suggesting a greater degree of environmental similarity compared to other species pairs (Table 3, Fig. 5A). In contrast, *A. lermaense* exhibited the lowest overlap with Bd (D = 0.038; I = 0.178), indicating limited environmental coincidence (Table 3, Fig. 5G). Interme-

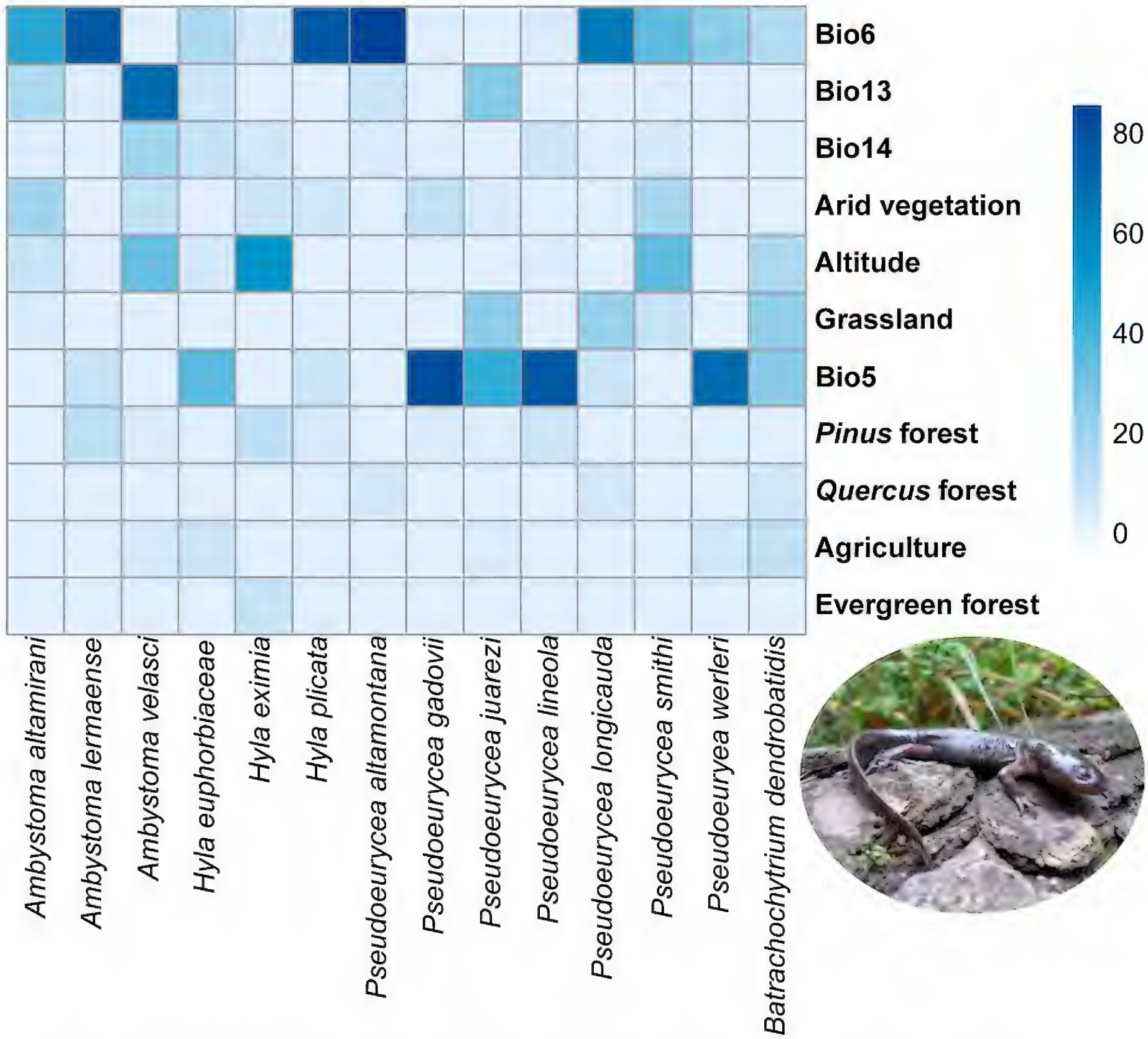

Figure 3. Variables that define the potential distribution of *Ambystoma*, *Pseudoeurycea* and *Hyla* species.

Table 2. Potential distribution percentages for each species.

Species	10th percentile training presence	80%
A. altamirani	44, 907.98	1368.47
A. lermaense	50, 481.14	730.07
A. velasci	234, 103.28	3686.08
H. euphorbiaceae	255, 506.59	3261.24
H. eximia	221, 008.07	1991.33
H. plicata	42, 368.39	1296.85
P. altamontana	9, 982.09	416.15
P. gadovii	51, 225.9	569.53
P. juarezi	24, 308.97	1719.04
P. lineola	33, 806.4	1385.48
P. longicauda	89, 756.25	1748.84
P. smithi	77, 338.12	1585.88
P. werleri	18, 777.4	676.63
B. dendrobatidis	267, 557.2	7087.28

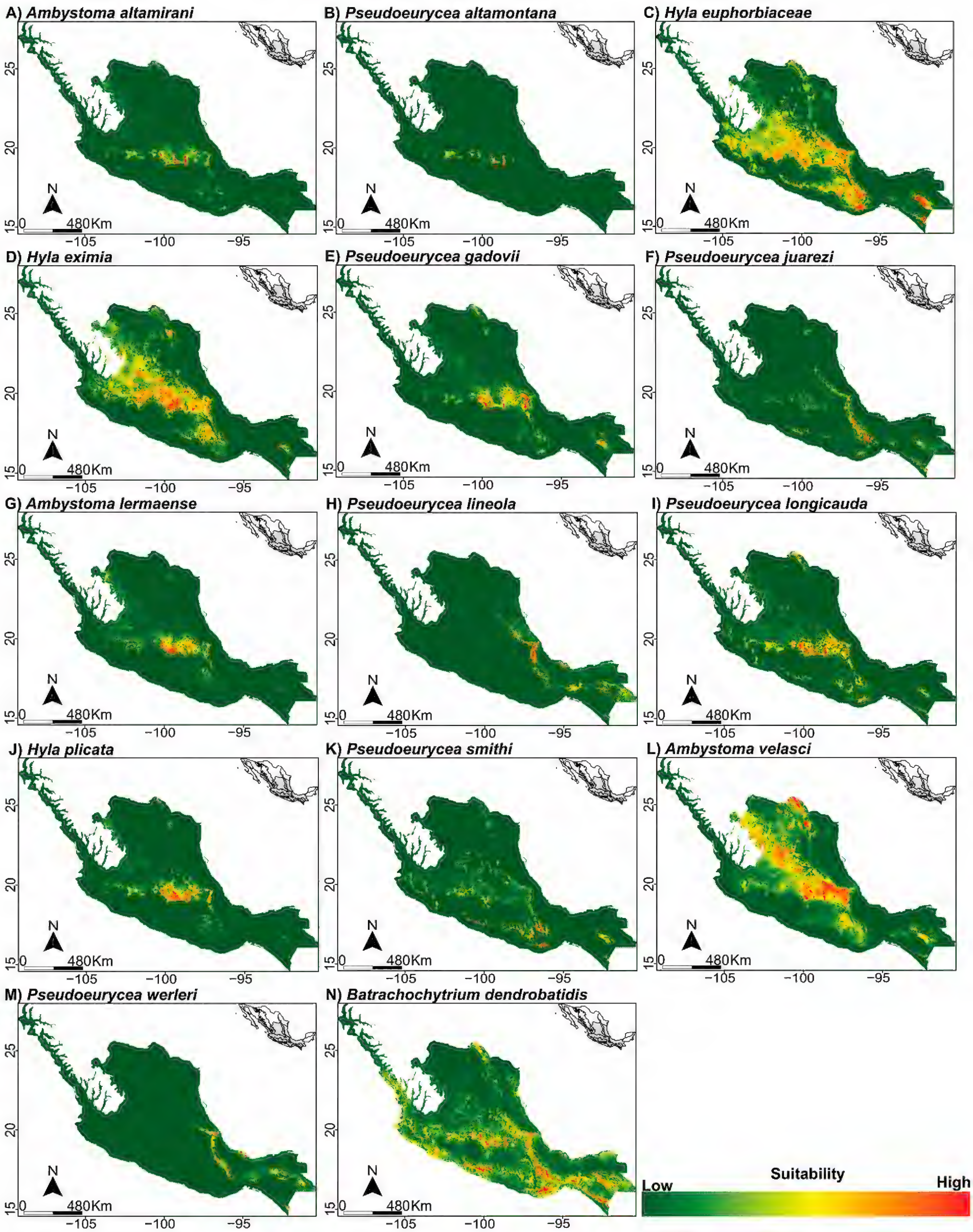

Figure 4. Potential distribution map of 14 amphibian species *Batrachochytrium dendrobatidis* determined using the Maxent algorithm implemented in ENMeval.

diate overlap values were observed for *Hyla plicata* (D = 0.367; I = 0.534) (Table 3, Fig. 5J), whereas lower overlap values characterised *H. eximia* (D = 0.088; I = 0.268) (Table 3, Fig. 5D). Within *Pseudoeurycea*, *P. altamontana* and *P. longicauda*

Table 3. Niche overlap between *B. dendrobatidis* and 14 amphibian species.

		D	I
B. dendrobatidis vs.	*A. altamirani*	0.423158; p = 0.06	0.5724754; p = 0.05
	P. altamontana	0.4150246; p = 0.07	0.5510623; p = 0.07
	H. euphorbiaceae	0.1249992; p = 0.15	0.3337388; p = 0.12
	H. eximia	0.08779066; p = 0.38	0.268212; p = 0.28
	P. gadovii	0.3640408; p = 0.17	0.4930263; p =0.16
	P. juarezi	0.3828691; p =0.37	0.5547978; p = 0.36
	A. lermaense	0.03783475; p = 0.23	0.1779129; p = 0.19
	P. lineola	0.1371793; p = 0.30	0.2830481; p = 0.29
	P. longicauda	0.4260345; p = 0.13	0.5924669; p = 0.22
	H. plicata	0.3669029; p = 0.15	0.5343388; p = 0.13
	P. smithi	0.34505; p = 0.26	0.579068; p = 0.21
	A. velasci	0.2575035; p = 0.20	0.4729941; p = 0.17
	P. werleri	0.0847936; p = 0.30	0.2038027; p = 0.38

Table 4. Linear blob and ribbon range break test results for *B. dendrobatidis* and 14 amphibian species in the environmental space. Schoener's D (Schoener 1970), I (Warren et al. 2008), env. D, env. I, env.cor. (Warren et al. 2021).

		D	I	Rank cor	Env cor	Env. D	Env. I
B. dendrobatidis vs.	*A. altamirani*	0.376	0.648	0.408	0.108	0.033	0.134
	P. altamontana	0.040	0.177	0.068	-0.037	0.003	0.010
	H. euphorbiaceae	0.585	0.817	0.567	0.182	0.031	0.148
	H. eximia	0.440	0.693	0.109	0.043	0.027	0.112
	P. gadovii	0.407	0.697	0.470	0.730	0.376	0.649
	P. juarezi	0.535	0.794	0.601	0.104	0.009	0.070
	A. lermaense	0.202	0.452	0.160	0.112	0.007	0.053
	P. lineola	0.349	0.606	0.453	0.120	0.010	0.088
	P. longicauda	0.337	0.585	0.254	0.060	0.004	0.036
	H. plicata	0.347	0.620	0.180	0.001	0.012	0.161
	P. smithi	0.623	0.849	0.636	0.079	0.004	0.043
	A. velasci	0.425	0.675	0.130	0.287	0.305	0.497
	P. werleri	0.011	0.077	0.154	0.490	0.373	0.583

showed comparatively higher overlap values with Bd, while *P. lineola* presented lower overlap values (Table 3, Fig. 5B, I, H). Based on environmental overlap metrics (env. D, env. I and env. cor.), species showing greater environmental coincidence with Bd included *H. euphorbiacea*, *H. eximia*, *H. plicata*, *A. altamirani*, *A. velasci*, *P. gadovii*, *P. juarezi*, *P. lineola*, *P. longicauda and P. smithi* (Table 4). When considering density values above 0.5, *A. altamirani*, *H. plicata*, *P. altamontana*, *P. longicauda* and *P. gadovii* exhibited broader environmental niches scaled by availability, suggesting greater potential environmental compatibility with Bd. Ribbon range break analyses identified three main geographic discontinuities in niche overlap and connectivity. The first was located in the Trans-Mexican Volcanic Belt at the boundary between Guanajuato and Querétaro, affecting Bd overlap with *H. plicata*, *A. altamirani*, *A. lermaense*, *P. gadovii*, *P. lineola* and *P. longicauda*.

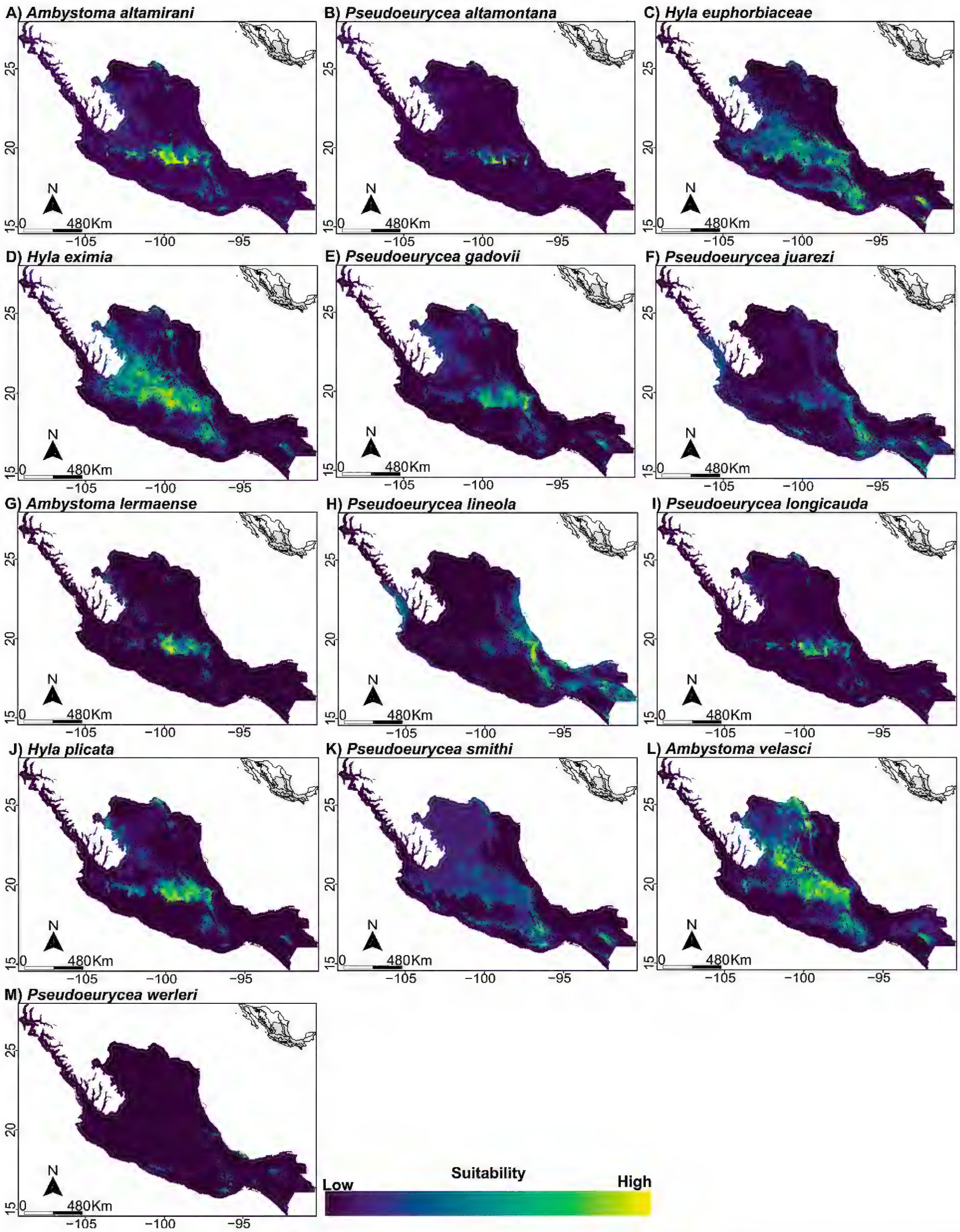

Figure 5. Potential distribution map of 14 amphibian species *Batrachochytrium dendrobatidis* determined using the ensemble algorithm implemented in biomod2.

A second break was detected in southern Puebla and a third in southern San Luis Potosí, influencing connectivity between Bd and *A. velasci* in the Altiplano Sur and between Bd and several *H. euphorbiacea* in northern Oaxaca and *Pseudoeurycea* species (*P. altamontana*, *P. juarezi*, *P. smithi*, *P. werleri*) (Fig. 6).

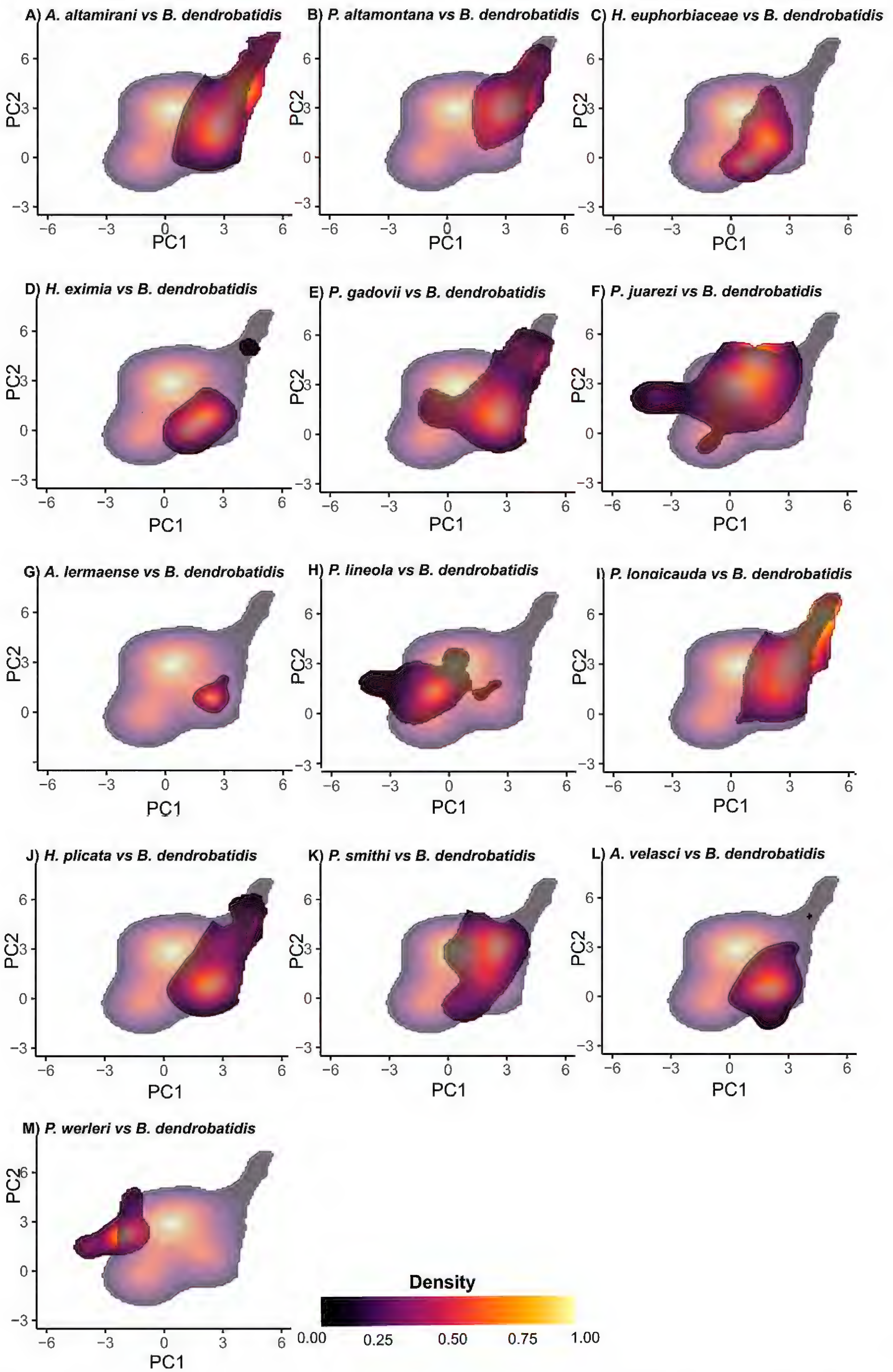
A) A. altamirani vs B. dendrobatidis
B) P. altamontana vs B. dendrobatidis
C) H. euphorbiaceae vs B. dendrobatidis
D) H. eximia vs B. dendrobatidis
E) P. gadovii vs B. dendrobatidis
F) P. juarezi vs B. dendrobatidis
G) A. lermaense vs B. dendrobatidis
H) P. lineola vs B. dendrobatidis
I) P. longicauda vs B. dendrobatidis
J) H. plicata vs B. dendrobatidis
K) P. smithi vs B. dendrobatidis
L) A. velasci vs B. dendrobatidis
M) P. werleri vs B. dendrobatidis
PC1
PC2
Density
0.00
0.25
0.50
0.75
1.00

Figure 6. Environmental niche overlap between *Batrachochytrium dendrobatidis* and each amphibian species.

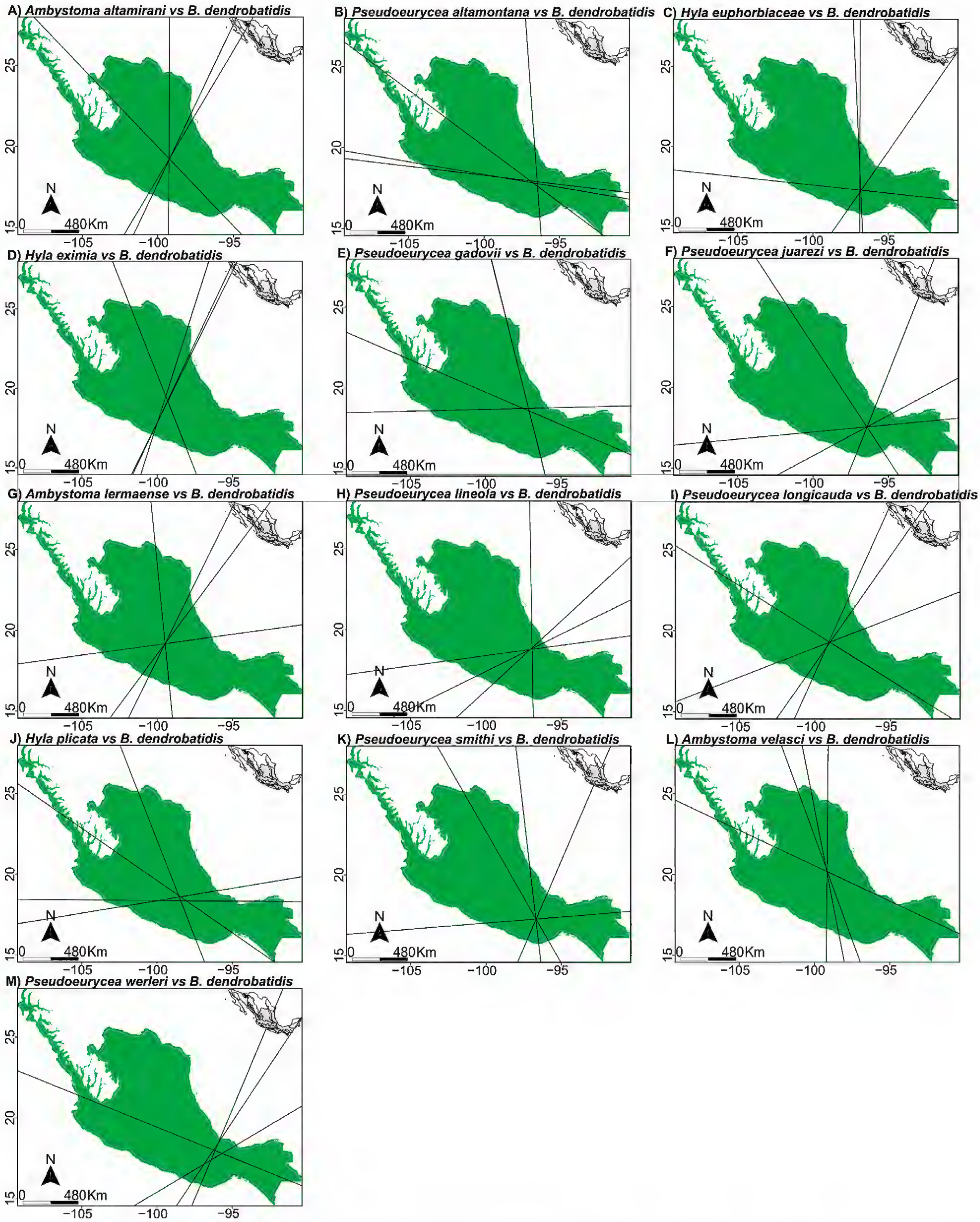
A) Ambystoma altamirani vs B. dendrobatidis
B) Pseudoeurycea altamontana vs B. dendrobatidis
C) Hyla euphorbiaceae vs B. dendrobatidis
D) Hyla eximia vs B. dendrobatidis
E) Pseudoeurycea gadovii vs B. dendrobatidis
F) Pseudoeurycea juarezi vs B. dendrobatidis
G) Ambystoma lermaense vs B. dendrobatidis
H) Pseudoeurycea lineola vs B. dendrobatidis
I) Pseudoeurycea longicauda vs B. dendrobatidis
J) Hyla plicata vs B. dendrobatidis
K) Pseudoeurycea smithi vs B. dendrobatidis
L) Ambystoma velasci vs B. dendrobatidis
M) Pseudoeurycea werleri vs B. dendrobatidis
N
0 480Km
15
20
25
−105
−100
−95

Figure 7. Ribbon and range-break test between *Batrachochytrium dendrobatidis* and 14 amphibian species.

Spatial overlap maps further revealed heterogeneous patterns of co-occurrence between Bd and the 13 amphibian species across the Trans-Mexican Volcanic Belt (Fig. 7). Areas of greater overlap were concentrated in central and southern Mexico, particularly within montane forest regions. Species such

as *Pseudoeurycea juarezi*, *P. longicauda* and *P. altamontana* exhibited more extensive overlap zones with Bd, especially along the eastern slopes of the Sierra Madre Oriental and southern volcanic ranges. In contrast, *Hyla eximia* and *Ambystoma velasci* showed more restricted overlap, primarily limited to isolated habitat patches. These spatial patterns highlight regions where amphibian populations may experience relatively higher potential exposure to Bd.

Barplot analysis (Fig. 8A) indicated that *P. juarezi*, *P. longicauda* and *P. altamontana* exhibited the highest percentage of spatial overlap with Bd, all exceeding 70% of their distribution ranges. Conversely, *A. velasci* and *H. eximia* had the lowest overlap, below 40%. When spatial overlap was combined with the IUCN conservation status, we calculated a vulnerability index (Fig. 8B), which ranked *P. altamontana*, *P. longicauda* and *P. juarezi* as the most vulnerable species. This index also revealed species with high overlap, but low IUCN concern (e.g. *P. juarezi*).

Principal Component Analysis, based on the vulnerability index and overlap data (Fig. 9), revealed clear separation amongst the species. PC1 explained 92.3% of the variance and was primarily driven by the percentage of overlap with Bd, while PC2 (7.7%) captured minor variations associated with IUCN status. Species grouped along a gradient from low (black) to high (yellow) vulnerability values. Notably, *Pseudoeurycea juarezi*, *P. longicauda* and *P. altamontana* formed a distinct cluster of highly vulnerable species located in the upper-right quadrant of the ordination space. These species are characterised by high Bd overlap and threatened IUCN categories. *A. lermaense*, *P. lineola* and *P. werleri* formed a cluster of moderately vulnerable species in the lower-right quadrant. In contrast, species such as *Ambystoma velasci* and *Hyla eximia* were positioned on the lower-left side of the plot, indicating lower spatial risk and different conservation contexts.

A species richness map (Fig. 10A) showed that amphibian diversity is highest in the central highlands of Mexico, particularly in regions overlapping with the Trans-Mexican Volcanic Belt, where richness values reach up to nine species per pixel. The overlay map (Fig. 10B) demonstrated that the suitability of Bd was notably high in these same regions. This spatial congruence suggests that biodiversity hotspots may coincide with areas of high disease risk, highlighting the urgent need for targeted surveillance and mitigation efforts in these overlapping zones.

Discussion

Ecological Niche Modelling

The Trans-Mexican Volcanic Belt (TMVB) and the Sierra Madre del Sur (SMS) emerged as the primary biogeographic regions with the highest potential distributions for the genera *Hyla*, *Pseudoeurycea* and *Ambystoma*. The TMVB is considered the core of the Mexican Transition Zone due to its role in connecting major biogeographic provinces, including the SMS, Sierra Madre Occidental (SMOcc), Sierra Madre Oriental (SMO) and the AS, thereby fostering highly diverse biota towards the south (Lemos-Espinal and Smith 2025a; Lemos-Espinal and Smith 2025b). Sierra Madre del Sur is a biogeographic province that harbours a remarkable diversity of amphibians: within this region, *H. euphorbiaceae*, *H. eximia*, *P. juarezi*,

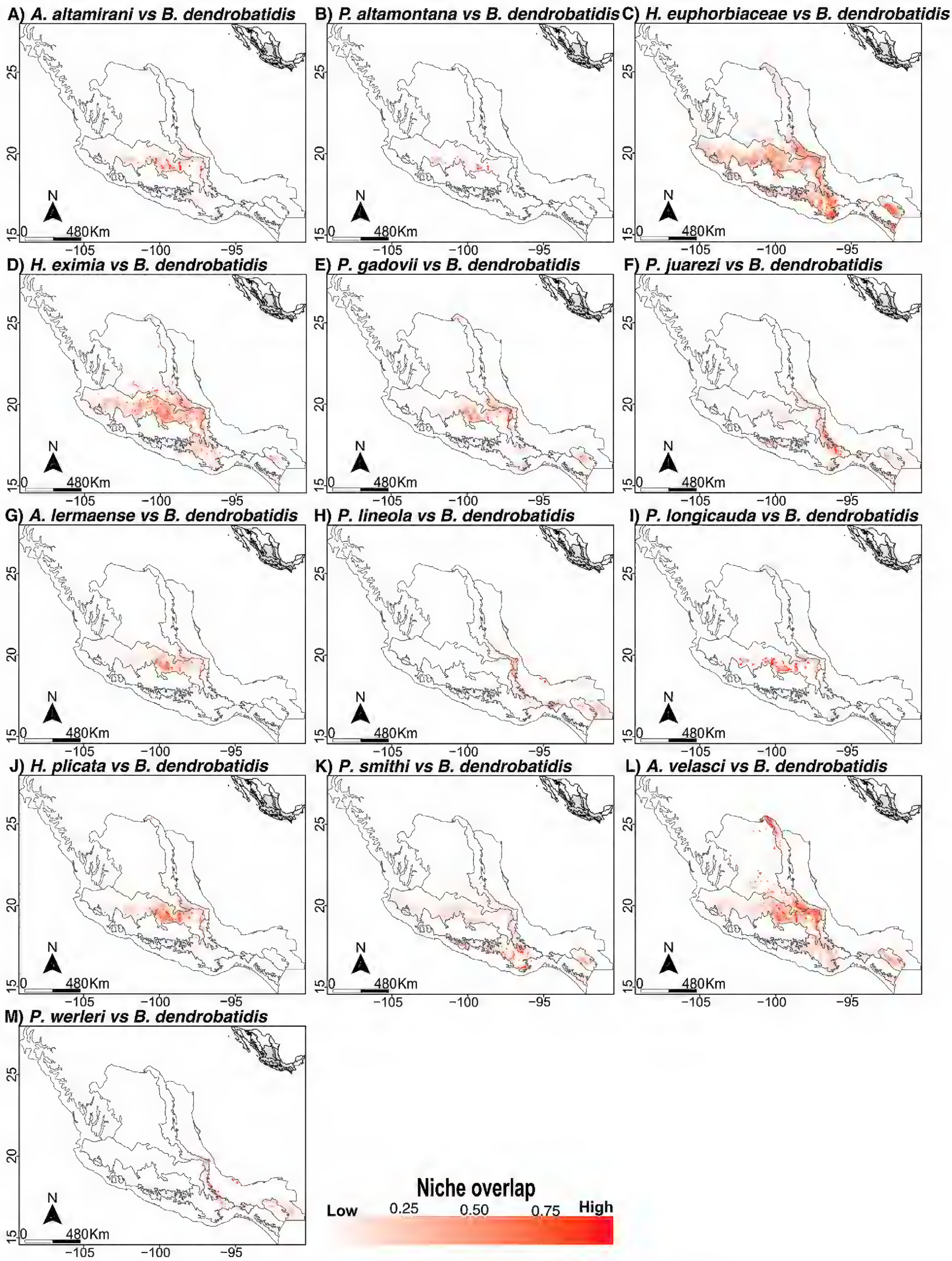

Figure 8. Spatial overlap between amphibian species and *Batrachochytrium dendrobatidis*.

P. smithi and *P. werleri* are well represented, while, to date, the genus *Ambystoma* is represented only by *A. velasci* (Lemos-Espinal and Smith 2025a). In contrast, the TMVB is notably rich in *Ambystoma* diversity, hosting at least 13 species, including

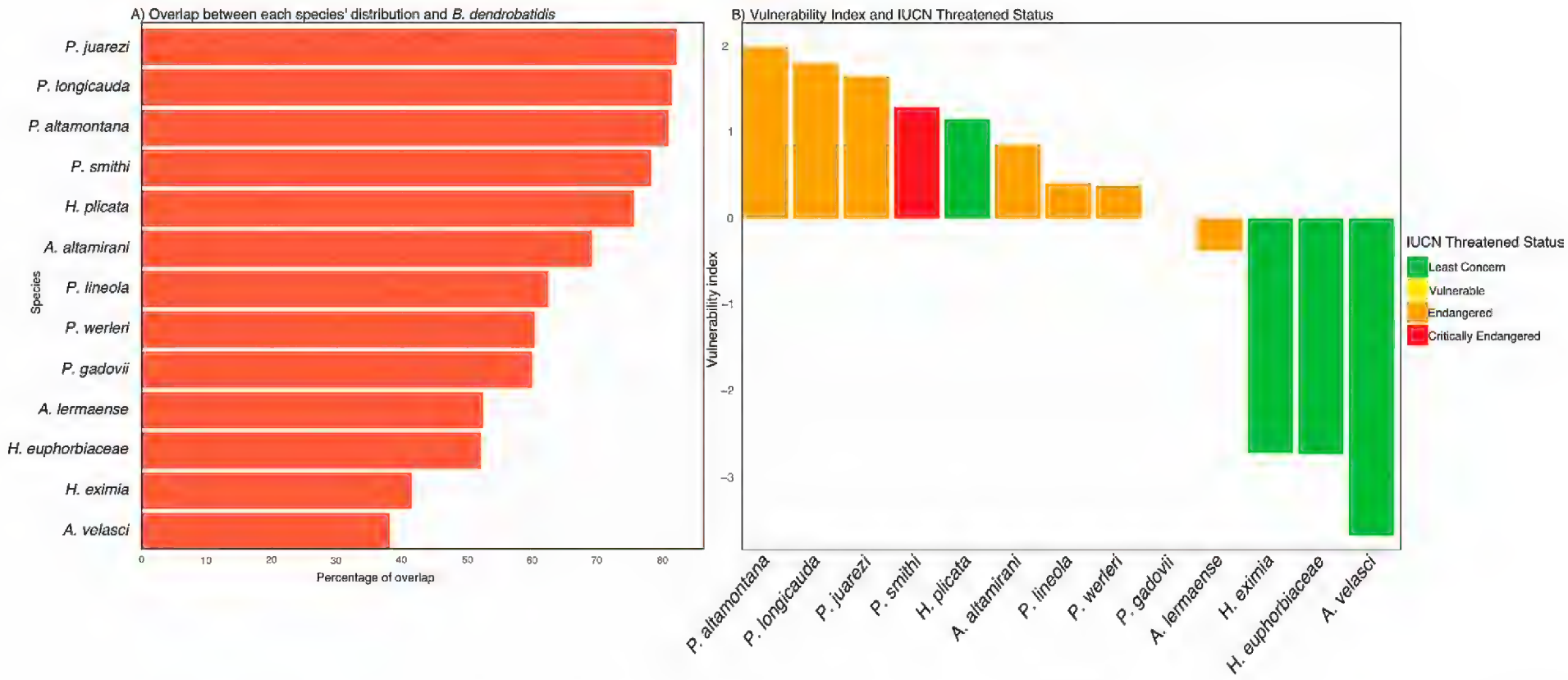

Figure 9. A. Barplot of the spatial overlap percentage between Bd and each species; **B.** Vulnerability index combining Bd overlap and IUCN status.

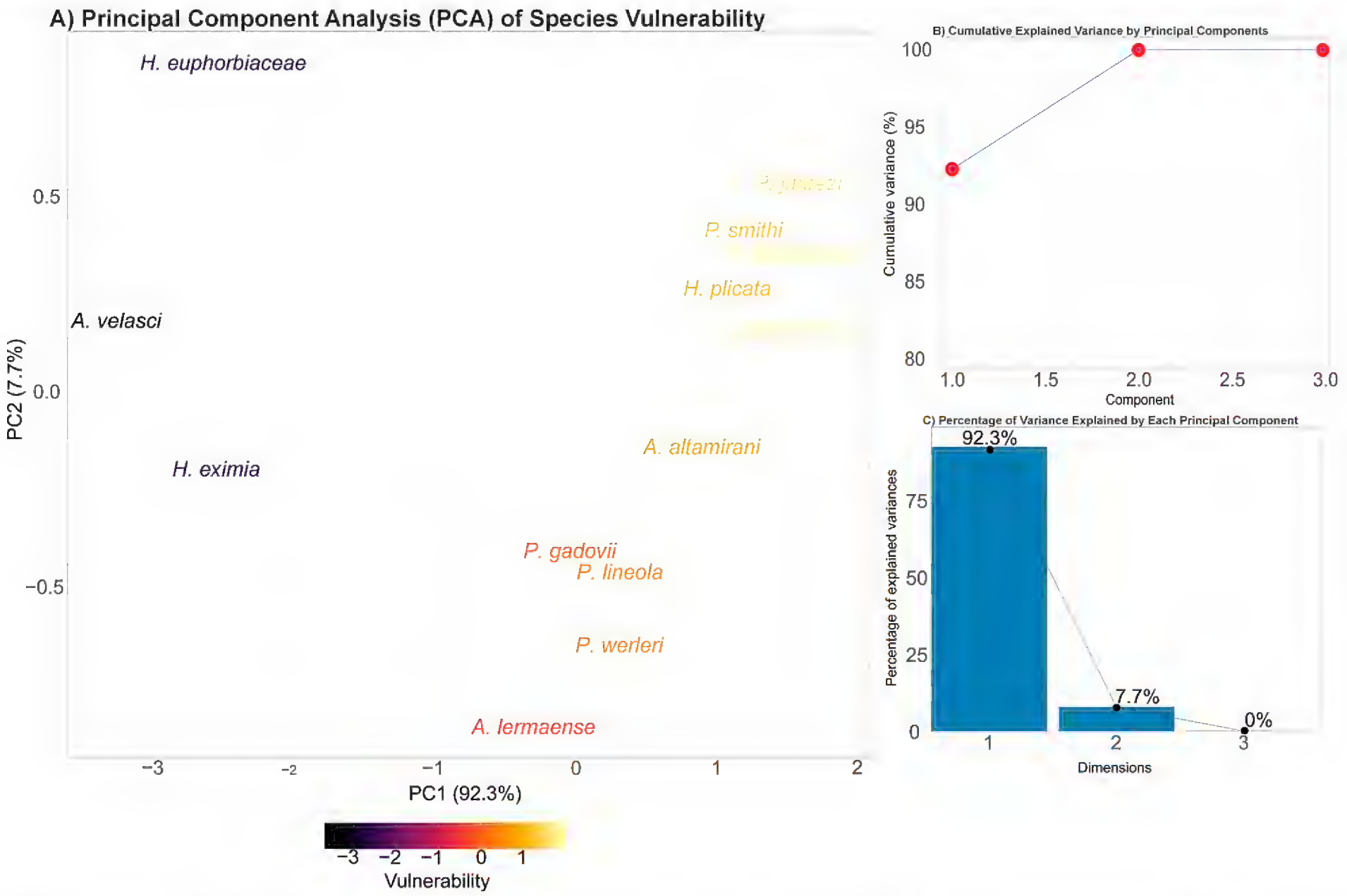

Figure 10. A. Principal component analysis (PCA) of species vulnerability to Bd; **B.** Cumulative explained variance by Principal components; **C.** Percentage of variance explained by each Principal component.

A. altamirani, *A. lermaense* and *A. velasci*. Although *P. juarezi*, *P. lineola*, *P. smithi* and *P. werleri* are absent from the TMVB, this biogeographic province contains at least 23 species of *Pseudoeurycea* and four species of *Hyla* (Lemos-Espinal and Smith 2024). The three *Hyla* species analysed in this study are widely distributed across the TMVB, as are 12 species of *Pseudoeurycea*, namely, *P. altamontana*,

P. gadovii and *P. longicauda*. Amongst those regions examined, the Altiplano Sur (AS) region had the lowest amphibian species richness. Only *A. velasci*, *H. eximia* and *H. plicata* were distributed in this area, which is notably characterised by a lack of comprehensive herpetofaunal inventories (Domínguez-Domínguez and Pérez-Ponce de León 2009; Lemos-Espinal et al. 2018; Leyte-Manrique et al. 2022).

Distribution of *Batrachochytrium dendrobatidis* and its potential impact

Batrachochytrium dendrobatidis exhibited a potential distribution across the three main biogeographic provinces identified in this study: the TMVB, the SMS and the AS. This spatial overlap suggested that Bd could co-occur with multiple amphibian species from the genera *Hyla*, *Ambystoma* and *Pseudoeurycea*, thereby posing a significant threat to these taxa.

Confirmed reports of Bd presence span several Mexican states, including Chiapas, Oaxaca, Guerrero, Morelos, Michoacán, Estado de México, Puebla, Ciudad de México, Hidalgo, Veracruz and Tamaulipas (Mendoza-Almeralla et al. 2015). In these States, Bd has been associated with infections in several species, such as *H. eximia*, *H. euphorbiacea*, *A. altamirani*, *A. lermaense*, *A. velasci*, *P. longicauda* and *P. smithi* (Cheng et al. 2011; Mendoza-Almeralla et al. 2015; Basanta et al. 2021), confirming the susceptibility of these species to chytridiomycosis. Moreover, other species not included in our niche models have also been reported as susceptible. These include *Isthmura belli*, *Pseudoeurycea cephalica*, *P. firscheini* and *P. leprosa* (Van Rooij et al. 2011), as well as *Ambystoma andersoni* and *A. flavipiperatum* (Basanta et al. 2019). These findings suggest that a broader range of species within these genera may be vulnerable to Bd infection.

However, some exceptions to susceptibility have been documented. For example, *A. velasci* form Alchichica Lake (formerly *A. taylori*) has been reported to be potentially resistant to Bd, possibly due to the high salinity of the lake in which it resides, which may inhibit the survival of the fungus (Parra-Olea et al. 2022; Frost et al. 2025). This highlights the importance of identifying resistant species or populations, as they may provide viable options for conservation and disease management strategies. The broad ecological tolerance of Bd further complicates mitigation efforts. It has been documented in a wide variety of

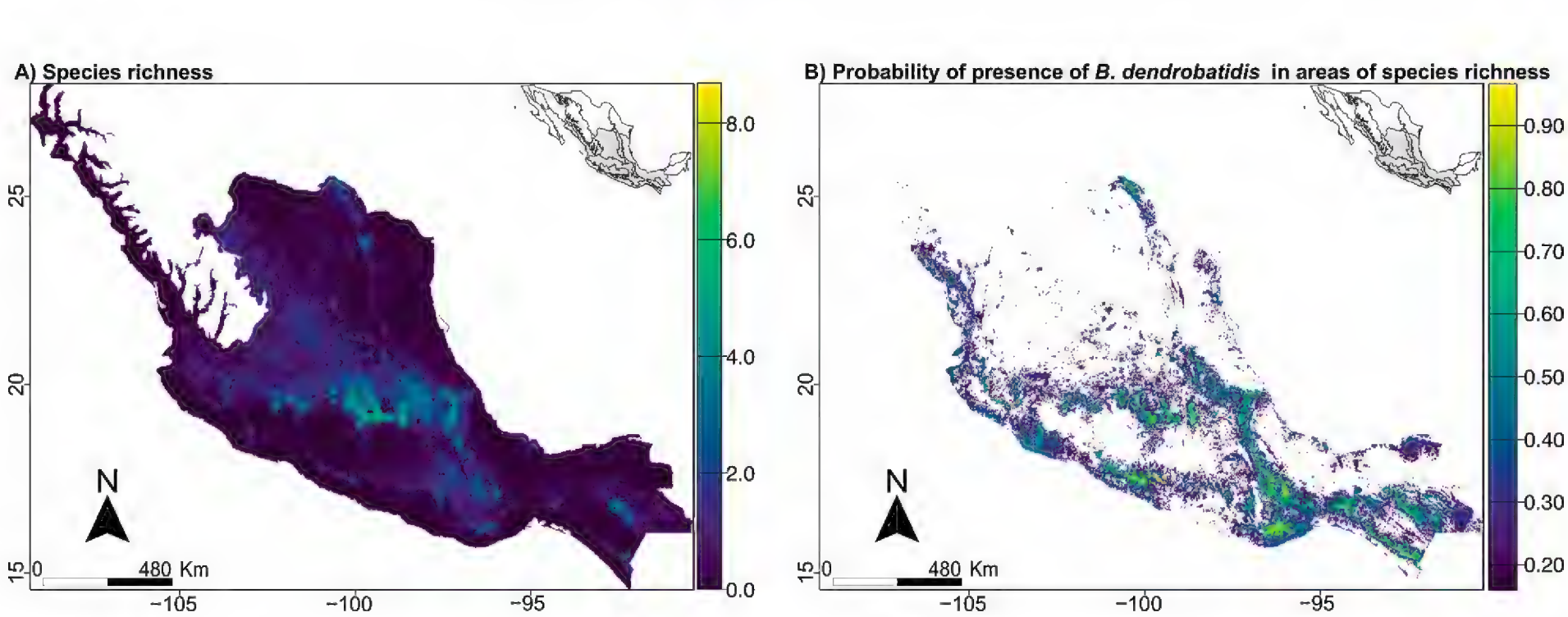

Figure 11. A. Species richness map of the 13 amphibian species; **B.** Spatial overlap between amphibian species richness and habitat suitability according to Bd.

habitats, ranging from high mountain regions to lowland environments, encompassing diverse climatic conditions. Its cosmopolitan distribution is further supported by population genetic studies, which reveal high genetic admixture and a lack of clear geographic structure across central and southern Mexico (Zumbado-Ulate et al. 2019; Basanta et al. 2021). These traits make containment of the fungus particularly challenging, underscoring the urgency of developing comprehensive monitoring and management strategies.

Environmental drivers of distribution patterns in *Hyla* and *Ambystoma*

A high probability of presence of the genus *Ambystoma* was associated with elevation as a positively influential variable. This correlation is likely due to the genus' highest species diversity occurring in the TMVB, a biogeographic zone characterised by mountainous terrain and cold climates. Within this region, *A. altamirani* occupies the highest altitudinal range (2,450–3,487 m a.s.l.), followed by *A. lermaense* (2,800–3,000 m a.s.l.), while A. *velasci* displays the broadest altitudinal range, from 1,800 to 3,000 m a.s.l. (AmphibiaWeb 2025). This latter species is distributed both in the TMVB and in the AS, highlighting its ecological plasticity. The minimum temperature of the coldest month (Bio6) was another significant predictor of *Ambystoma* distribution, with suitability ranges spanning from 0 to 20 °C. *Ambystoma altamirani* occurs predominantly in the coldest conditions within this range, whereas *A. velasci* occupies the warmer end. The reported optimal temperature ranges for this genus lie between 12 °C and 17 °C (Lemos-Espinal et al. 2016; Sánchez-Sánchez et al. 2024; Vargas-Gómez and Chaparro-Herrera 2024).

Although the *Abies* forest variable showed low permutation importance in the models, its ecological relevance is underscored by both our findings and literature which indicate that the presence of *A. altamirani* is strongly linked to these forest habitats and that *A. velasci*, although it has been reported from a variety of habitats, including semi-arid regions, our results suggest also a local association with *Abies* forests and this association may reflect regional ecological conditions rather than the species' full ecological breadth (Heredia-Bobadilla et al. 2016, 2017; Sunny et al. 2024a; AmphibiaWeb 2025). Additionally, precipitation variables – specifically, the wettest and driest months – emerged as key factors. Rainfall patterns have a direct influence on reproductive events such as egg laying and larval abundance in *Ambystoma*, which tend to peak during the rainy season (Lemos-Espinal et al. 2017; Escalera-Vázquez et al. 2018). The life history traits of anurans, particularly those in the genus *Hyla*, are tightly linked to both temperature and precipitation (Hernández-Salinas et al. 2018). Precipitation during the driest month was an important determinant of habitat suitability for *H. euphorbiacea* and *H. eximia*, both of which exhibited high potential distributions in the AS, TMVB and SMS habitats under cool, high-elevation climates. These species rely heavily on seasonal rainfall to trigger reproductive behaviour such as mating calls and amplexus (Cruz-Ruiz et al. 2015; Lemos-Espinal et al. 2016; Hernández-Salinas et al. 2018). While rainfall is also crucial for *H. plicata*, its habitat suitability appears to be more strongly influenced by temperature extremes – both maximum and minimum. This pattern is also observed in *H. euphorbiacea*, indicating that temperature plays a critical role in anuran development (Manjarrez 1994).

Notably, temperature variability across the TMVB and SMS has been well documented (Villers-Ruiz and Castañeda-Aguado 2013; Sáenz-Romero et al. 2020; Sánchez-Velásquez et al. 2023; Wootton et al. 2023). This variability is significant for *Hyla* distributions, as these species are considered highly adaptable. It has been proposed that hylids originated in tropical environments and subsequently adapted to temperate regions through long-term evolutionary processes (Wiens et al. 2006; Cruz-Ruiz et al. 2015). However, the current process of climate change is so rapid that climate change may outstrip the adaptive capacity of these species, posing a significant threat to their persistence.

Distribution of environmental determinants of *Pseudoeurycea* and *Batrachochytrium dendrobatidis*

Species within the genus *Pseudoeurycea* displayed high habitat suitability primarily within the TMVB and, more notably, in the SMS, where 23 species have been described (Rovito et al. 2015). For *P. juarezi*, habitat suitability was influenced mainly by the maximum temperature in the warmest month, whereas, for *P. altamontana* and *P. smithi*, the minimum temperature in the coldest month was the most significant predictor. The remaining species exhibited sensitivity to both temperature extremes. These results reinforce previous findings that temperature is a key ecological driver for salamanders (Friedman and Muñoz 2022), as the physiology of plethodontids is closely adapted to the climatic conditions of their geographic range (Clay and Gifford 2018). Precipitation also played a critical role. The wettest and driest months were important for *P. altamontana* and *P. smithi*, while the habitat suitability of the other species was influenced primarily by precipitation during the driest month. This finding is consistent with the natural history of *Pseudoeurycea*, whose members spend most of their time decomposing logs or within burrows, where even limited rainfall during dry months helps maintain the humidity of these crucial microhabitats (Solano-Zavaleta et al. 2009; Sunny et al. 2021).

Abies-Pinus forests were also found to be significant in determining habitat suitability for several species. For example, *H. eximia*, *H. plicata*, *P. gadovii* and *P. juarezi* showed strong associations with this vegetation type. The suitable areas for *H. eximia* and *H. plicata* were primarily located in the AS and TMVB, with *Pinus* forests being more prevalent in the TMVB (Aguilar-Zúñiga et al. 2008). On the other hand, *P. gadovii* was distributed across the TMVB and Oaxaca, particularly in areas such as the Parque Nacional Cofre de Perote and the Sierra Juárez, where the dominant vegetation types include *Pinus*, *Quercus* and *Abies* forests (Zacarías-Eslava and del Castillo 2010).

Interestingly, the environmental variables that influence amphibian distributions also shape the habitat suitability of Bd. The maximum temperature of the warmest month and the minimum temperature of the coldest month were both significant predictors, with the latter showing a negative relationship. Our results indicate that the optimal temperature range for Bd lies between 10 °C and 25 °C, which aligns with observations from European studies (Nie and Feng 2022; Tytar et al. 2023; Thumsová et al. 2025).

Elevation was also a key variable; Bd has been detected in virtually every amphibian-inhabited region of Mexico, ranging from 1 - 3,300 m a.s.l. (Bolom-Huet et al. 2019; Nie and Feng 2022). Notably, the species examined in this study –

Hyla, *Ambystoma* and *Pseudoeurycea* – occupy elevations between 900 m and 3,487 m a.s.l. (AmphibiaWeb 2025), indicating substantial overlap with the fungus range. Surprisingly, Bd has also been reported in high-elevation mountains, despite expectations that extreme climatic conditions would limit its presence (Nava-González et al. 2019).

Additionally, *Quercus* forests emerged as important for Bd distribution. These temperate forests typically exhibit temperatures ranging between ~ 12 °C and 18 °C (Figueroa-Rangel and Olvera-Vargas 2022), conditions that are ideal for Bd and provide habitat for *H. euphorbiacea*, *A. velasci*, *P. juarezi* and *P. smithi* (AmphibiaWeb 2025). The convergence of suitable climatic conditions and host presence makes these forests potential hotspots for Bd proliferation (Gómez-Benitez et al. 2025).

Niche overlap and vulnerability of amphibians to *Batrachochytrium dendrobatidis*

The pathogenic fungus Bd showed environmental niche overlap with most of the amphibian species modelled in this study. However, because the majority of niche similarity tests yielded non-significant p-values ($p > 0.05$), these results are interpreted within a qualitative and comparative framework, based on the magnitude and spatial patterns of niche overlap, rather than as statistically significant similarity.

Working with host–pathogen systems inherently involves the use of data that are not fully spatially independent. This is expected, as wildlife disease dynamics depend on host movements and ecological interactions that facilitate pathogen transmission or limit its spread (Vargas-Soto et al. 2025). Consequently, the origin and structure of occurrence data must be carefully considered to avoid overestimating niche overlap. To minimise potential biases, all presence records were standardised to the same temporal period and all databases were cleaned following identical procedures. Amphibian and Bd occurrence records were compiled from different sources to capture the broadest possible range of geographic and environmental conditions for both hosts and pathogen. *Batrachochytrium dendrobatidis* presence records were derived from field surveys conducted at sites reporting chytridiomycosis, as well as from published studies combining field sampling with confirmed molecular detections (e.g. qPCR; Bolom-Huerta et al. (2019)).

Amongst the species evaluated, *Ambystoma altamirani* exhibited comparatively higher niche overlap values with Bd, indicating a greater degree of environmental coincidence relative to other species. This pattern suggests that *A. altamirani* may experience elevated potential exposure to Bd under current environmental conditions. Consistent with this interpretation, reports of Bd-infected populations of *A. altamirani* have increased in recent years (Frías-Álvarez et al. 2008; Basanta et al. 2021; Basanta et al. 2022; Martínez-Ugalde et al. 2022). Species of the genus *Ambystoma* may be particularly susceptible due to their facultative life cycles, which involve prolonged use of aquatic habitats that promote fungal persistence through sustained moisture availability (Nava-González et al. 2020).

In contrast, although *Ambystoma ordinarium* and *Ambystoma altamirani* (formerly *A. rivulare*) have been reported as Bd-positive without overt clinical symptoms, suggesting that local microhabitat conditions and elevation may

influence infection severity (Nava-González et al. 2020; Mendoza-Almeralla et al. 2023), there are currently no confirmed reports of Bd infection in *Ambystoma lermaense*. This absence of evidence likely reflects limited sampling or research effort rather than true resistance or absence of infection. Overall, these findings emphasise that observed niche overlap patterns represent potential environmental compatibility and exposure risk, rather than definitive evidence of statistically significant niche similarity.

Range break analyses revealed potential barriers to Bd dispersal, particularly around AS, which could harbour *A. velasci* and *Hyla eximia* populations free from Bd. Although isolated cases of infection have been reported in Puebla and Guanajuato (Frías-Álvarez et al. 2008; Leyte-Manrique et al. 2023), Oaxaca (particularly in Sierra de Juárez) – recognised as Alliance for Zero Extinction sites – show very limited Bd presence. In these areas, the pathogen has been detected in only a few individuals of *Craugastor* spp. (Cabrera-Hernández 2012), which may indicate the success of conservation strategies in these zones, particularly within natural protected areas and priority conservation regions (Ceballos 2009). As expected, the niche overlap between Bd and *Hyla*, *Ambystoma* and *Pseudoeurycea* species was high, especially within the TMVB and SMS biogeographic regions. Therefore, targeted monitoring efforts should prioritise species already known to be affected by chytridiomycosis in these zones, such as *H. euphorbiacea*, *H. eximia*, *A. altamirani*, *A. lermaense*, *A. velasci*, *P. longicauda* and *P. smithi*, particularly in *Quercus*-dominated forests.

Catastrophic amphibian declines associated with chytridiomycosis are closely linked to anthropogenic disturbances (Lips et al. 2006; Fisher et al. 2012). Efficient resource allocation for disease surveillance will help to establish restricted-access zones and reduce activities, such as ecotourism, which may facilitate pathogen spread. It is worth noting that the current natural protected areas in the TMVB and SMS are insufficient to encompass the full range of amphibian biodiversity. In many cases, endemic species occur outside these designated zones (González-Fernández et al. 2022), undermining conservation efforts. Community-based conservation initiatives and voluntary reserves managed by indigenous people (Almazán-Núñez et al. 2011; Peña-Azcona et al. 2022) offer an opportunity to expand protected areas and implement habitat restoration and environmental education programmes. These initiatives are particularly important in range break zones, which may act as natural barriers against Bd dissemination.

Deforestation poses a critical threat in the TMVB and SMS regions, with *Abies*, *Pinus* and *Quercus* forests experiencing the greatest impact (Aguilar-Tomasini et al. 2020; García-Jiménez and Vargas-Rodríguez 2021). Habitat loss not only disrupts amphibian distributions, but also alters climatic and microclimatic conditions. Rising temperatures – often associated with deforestation — are amongst the primary climatic factors that favour Bd persistence. Thus, intensified efforts to prevent deforestation and enforce environmental protection laws are urgently needed. Our spatial overlap maps revealed heterogeneous co-occurrence patterns between Bd and the 13 modelled amphibian species. The highest overlap values were concentrated in the montane forests of central and southern Mexico.

Pseudoeurycea altamontana, *P. juarezi* and *P. longicauda* showed extensive overlap with Bd, particularly in the Sierra Madre Oriental and volcanic highlands. In contrast, species such as *H. eximia* and *A. velasci* exhibited more restricted overlap. Barplot analysis confirmed that *P. altamontana*, *P. juarezi* and *P. longicauda* exhibit-

ed the highest spatial overlap with Bd (> 70%), while *A. velasci* and *H. eximia* exhibited the lowest spatial overlap (< 40%). To integrate these data, we developed a vulnerability index that combines spatial overlap information with information from the IUCN Red List. This composite measure identified *P. altamontana*, *P. juarezi* and *P. longicauda* as the most vulnerable species and was characterised by high Bd exposure and elevated conservation concern. Principal component analysis (PCA) of vulnerability patterns revealed distinct species segregation. Species were grouped into three vulnerability clusters: (1) high-risk species (*P. altamontana*, *P. juarezi* and *P. longicauda*); (2) moderate-risk species (*P. lermaense*, *P. lineola* and *P. werleri*) and (3) low-risk species (*H. eximia* and *A. velasci*), possibly buffered by geographic or ecological traits. Finally, maps of amphibian species richness showed biodiversity peaks in the TMVB, which coincided spatially with areas of high Bd habitat suitability. This convergence highlights the urgent need for proactive Bd monitoring and conservation interventions in amphibian biodiversity hotspots.

Conservation implications

Our findings underscore the urgent need for integrated conservation strategies that address both biodiversity hotspots and emerging disease threats in central and southern Mexico. The Trans-Mexican Volcanic Belt and the Sierra Madre del Sur emerged as regions of exceptional amphibian richness and endemism, as well as areas with high environmental suitability for Bd. This spatial overlap represents a critical conservation concern, particularly for narrow-range species such as *Pseudoeurycea altamontana*, *P. juarezi* and *P. longicauda*, whose vulnerability indices we identified as the most at risk.

Although we did not explicitly assess the coverage or effectiveness of natural protected areas (NPAs), our spatial models suggest that many amphibian populations with high Bd exposure fall outside the boundaries of currently known protected zones. Previous studies have highlighted that NPAs in Mexico often fail to encompass the full distribution of amphibian endemism (González-Fernández et al. 2022), especially in mid- to high-elevation montane habitats. Therefore, additional efforts are needed to expand the conservation network, especially in areas identified in our maps as range break zones or Bd-free refugia, such as AS and Oaxaca.

Complementary conservation approaches – such as community-managed reserves, indigenous conservation territories and voluntary conservation areas could be essential for protecting amphibian diversity and mitigating Bd spread. In particular, regions near identified range breaks may serve as natural barriers or refugia where disease prevalence is low, making them strategic areas for monitoring and prevention. Given the role of microhabitats in modulating Bd severity, the conservation of forested landscapes – especially those dominated by *Abies*, *Quercus* and *Pinus* – becomes even more critical. These ecosystems provide both suitable amphibian habitats and favourable microclimates for Bd persistence. Protecting microhabitats such as shaded stream-banks, fallen logs and leaf litter is key to maintaining humidity refuges essential for both salamanders and frogs, while potentially buffering Bd proliferation.

Environmental education programmes focused on local communities are also crucial. Raising awareness about chytridiomycosis, promoting responsible ecotourism and encouraging habitat stewardship can strengthen grassroots

conservation. Furthermore, the identification of resistant or resilient amphibian populations – such as asymptomatic individuals of *Ambystoma ordinarium* or *A. altamirani* – may open avenues for conservation breeding programmes and disease mitigation strategies. Finally, integrating genetic, ecological and spatial data will be fundamental to developing adaptive, evidence-based management plans. In light of ongoing climate change, land-use pressures and disease emergence, proactive conservation strategies will be essential to safeguard Mexico's rich, but increasingly threatened amphibian diversity.

Conclusions

Our study provides a spatially-explicit assessment of the overlap between suitable habitats for endemic amphibian species and the chytrid fungus (Bd) in central and southern Mexico. Using ecological niche models, we identified areas of high conservation concern, particularly within the TMVB and the SMS, which host both high amphibian richness and favourable environmental conditions for Bd occurrence. We found that salamanders of the genus *Pseudoeurycea* exhibit the highest vulnerability due to their narrow geographic ranges, high overlap with Bd and threatened conservation status. In contrast, species, such as *Ambystoma velasci* and *Hyla eximia*, exhibited more restricted overlap, potentially due to geographic, ecological or physiological factors. A principal component analysis of vulnerability patterns revealed distinct clusters, allowing us to prioritise species and regions for conservation actions. Our findings also highlight the potential importance of range break zones – such Oaxaca and the AS – as natural barriers that could limit Bd spread. While these areas were not evaluated for disease presence in the field, their identification through modelling offers valuable hypotheses for future monitoring and targeted protection. Although we did not conduct explicit field assessments of Bd incidence or analyse the effectiveness of PAs, our spatial overlap maps, richness analyses and vulnerability indices offer a foundation for evidence-based prioritisation. These results can provide information for future research and conservation strategies aimed at mitigating disease risk in amphibian populations. However, further studies are urgently needed to evaluate the prevalence of Bd in under-sampled species (e.g. *Ambystoma lermaense*), explore the role of microhabitats and elevation in determining disease severity and model future distribution scenarios under climate change. Additionally, identifying potentially resistant amphibian lineages could contribute to proactive conservation strategies, including ex situ management and habitat restoration. In summary, our modelling framework offers a valuable tool for identifying species at greatest risk from chytridiomycosis and for guiding conservation efforts in Mexico's amphibian-rich montane regions. Coordinated actions that involve combined monitoring, habitat protection and community engagement will be essential for confronting the dual threats of habitat loss and emerging infectious disease.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following:
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Author contributions

Rosa Laura Heredia-Bobadilla and Armando Sunny conceptualized and led the project, secured funding, and coordinated the research activities.

Javier Manjarrez, Aldo Gómez-Benítez, Erika Adriana Reyes-Velázquez, Juan Manuel Carmen-Cristobal, Alexis Josué Sánchez-Lara, and Germán Martínez-Alva contributed equally to data compilation, spatial modeling, statistical analyses, and interpretation of results.

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Data availability

All of the data that support the findings of this study are available in the main text.